Original Article



Avian Abundance and Reproductive Success in the Intermountain West: Local-Scale Response to the Conservation Reserve Program

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ABSTRACT Conversion of extensive shrubsteppe communities to cropland has greatly reduced the habitat available to grassland- and sagebrush-obligate birds in the Intermountain West of the United States. In Washington State, approximately 600,000 ha of converted farmland have been planted to perennial grasses, forbs, and shrubs under the Conservation Reserve Program (CRP), currently the largest-scale effort creating perennial grassland habitat in this region. From 2003 to 2005 we sampled breeding birds and vegetation characteristics on 48 study sites in CRP and in native shrubsteppe. We used generalized linear models to examine characteristics associated with avian abundance and reproductive success. Abundance of shrubland and grassland birds was more closely associated with site vegetation than either management (planting of native vs. exotic grasses) or landscape factors, with cover of shrubs the dominant variable both for shrubland (positive effect) and for grassland (negative effect) birds. Daily survival rate of 1,377 nests in CRP was equal to or greater than that for nests in shrubsteppe and was similar for CRP planted with native versus exotic grasses. Seasonal reproductive success (young/breeding pair) of 2 focal species-Brewer's sparrow (Spizella breweri; n = 81 pairs) and Savannah sparrow (Passerculus sandwichensis; n = 58)—also was similar between CRP and native shrubsteppe. The CRP has the potential to significantly increase habitat available to shrubland and grassland birds in the Intermountain West and to increase local populations. Because shrubs take significantly longer than herbaceous plants to achieve a size beneficial to birds, CRP grasslands with a well-developed sagebrush (Artemisia spp.) component should be viewed as a long-term investment. © 2015 The Wildlife Society.

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Land-use changes across the globe have created vast agricultural landscapes that depart in significant ways from the natural landscapes that preceded them (Saunders et al. 1991, Foley et al. 2005). In North America, cultivation of short- and long-grass prairie ecosystems and the resultant shift from perennial grassland to annual cropland has been identified as a major factor in the decline of native grassland avifauna (Knopf 1994, Vickery et al. 1999, Brennan and Kuvlesky 2005). Similar loss of semiarid shrubsteppe ecosystems in western North America is believed to have resulted in the decline of numerous shrubland birds,

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²Present address: National Science Foundation, 4201 Wilson Boulevard, Suite 965, Arlington, VA 22230, USA ³Present address: New Mexico State University, College of Business, MSC 3CQ, P.O. Box 30001, Las Cruces, NM 88003, USA including several sagebrush obligates (Saab and Rich 1997, Paige and Ritter 1999, Knick et al. 2003) and has led to the proposed listing of the greater sage-grouse (*Centrocercus urophasianus*) under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2010). Invasion by nonnative grasses following wildfire poses an additional and more pervasive threat in aridland systems and has further reduced the amount of extant shrubsteppe on the landscape (D'Antonio and Vitousek 1992, Knick and Rotenberry 1997). In both of these ecosystems the loss of native habitat is exacerbated by fragmentation of the remaining grasslands and shrublands, with negative effects on area-sensitive species (Johnson and Igl 2001, Knick et al. 2003, Vander Haegen 2007).

The Conservation Reserve Program (CRP) is currently the largest-scale effort creating perennial grassland habitat in western North America. Administered by the U.S. Department of Agriculture, this voluntary program pays farmers to take agricultural lands out of production for a period of ≥ 10

conservation program is providing grassland and shrubland habitat at a spatial scale unlikely to be achieved by other means: in 2011, >12,000,000 ha of former cropland were enrolled in the program, mainly as perennial grassland (U.S. Department of Agriculture 2011). Moreover, these conservation lands occur primarily on private lands, in landscapes often dominated by tilled cropland and likely to remain so. It is widely recognized that conservation actions on public lands alone will be insufficient to meet many pressing conservation objectives (Noss and Peters 1995, Knight 1999). The potential for farmland set-aside programs, such as the CRP and the Permanent Cover Program in Canada (McMaster and Davis 2001) to aid populations of grassland

years to achieve conservation objectives, including reducing

soil erosion and providing wildlife habitat. Although sites are

planted with both native and nonnative species, this

CRP and the Permanent Cover Program in Canada (McMaster and Davis 2001), to aid populations of grassland birds was recognized early and has been the focus of considerable research (reviews in Johnson 2000, 2005, Jones-Farrand et al. 2007). Studies have documented use of individual restored fields by grassland birds and the vegetation characteristics that promote use (e.g., Johnson and Schwartz 1993, Patterson and Best 1996, McCoy et al. 2001, Van Buskirk and Willi 2004). At a larger scale, studies have associated occurrence of numerous grassland bird species with the presence or proportion of restored grasslands on the landscape (O'Conner et al. 1999), while others have associated regional trends in grassland bird populations with the amount of restored grasslands on the landscape (Haroldson et al. 2006, Veech 2006, Niemuth et al. 2007, Nielson et al. 2008). The general finding in most of these studies has been an increase in native grassland birds where restored grasslands are a part of the landscape.

The shrubsteppe of the Intermountain West occurs along a gradient from grassland to shrubland, largely as a result of rainfall, topographic and edaphic factors, and natural succession following wildfire (Daubenmire 1970). This gradient supports a range of bird species that are associated to a large degree with varying cover of shrubs (Wiens and Rotenberry 1981, Wiens et al. 1987, Earnst and Homes 2012). Conservation Reserve Program fields in this region differ from those in most other parts of the country in that they occur on lands that formerly supported vegetation communities with a significant shrub component, particularly sagebrush (Artemisia spp.). Mature sagebrush is a prerequisite for sagebrush-obligate birds (Braun et al. 1976, Knick et al. 2003) and a key element for other species that require shrubs for part of their life cycle (Johnson and O'Neil 2001). Species that depend on shrubs for food or nesting are largely excluded from grass-only fields, making planting of shrubs or natural seeding of shrubs from adjacent habitat a necessity. While greater sage-grouse have shown a positive response to CRP in Washington State (Schroeder and Vander Haegen 2011), USA, little is known concerning the use of these new habitats by other shrubsteppe and grassland wildlife in the Intermountain West or their potential to increase regional populations.

The goal of our study was to assess the potential for fields enrolled in the CRP to support bird species of conservation concern in the Intermountain West region. Specifically, we asked 1) how does abundance of birds in CRP fields compare with that in native shrubsteppe, 2) what are the relative effects of landscape composition, local vegetation structure, and local vegetation composition on avian abundance, and 3) what are the relative effects of vegetation structure and composition on rates of nest survival and seasonal reproductive success of key species?

STUDY AREA

The study took place in eastern Washington, within the geographic region known as the Columbia Basin. The region is characterized by hot, dry summers, and cold winters. Precipitation falls mainly during winter with annual totals ranging from 15 to 55 cm, increasing with elevation across the study area (Daubenmire 1970). Within the study area, topography is generally flat to rolling, with elevations ranging from approximately 750 m in the north to <250 m in some areas in the south (Daubenmire 1970).

Historically, most of the land in the study area supported shrubsteppe vegetation communities that ranged from bunchgrass-dominated steppe to sagebrush and antelope bitterbrush (*Purshia tridentata*) shrublands (Daubenmire 1970). Large-scale clearing of land for agriculture began in the late 1800s and expanded when irrigation became widespread after damming of the Columbia River in the 1930s (National Research Council 1995). Approximately 30% of the general study area currently is farmed (Jacobson and Snyder 2000), with dryland wheat the main crop in higher rainfall zones, whereas irrigated orchards, vineyards, and row crops prevail at lower elevations. Grazing by livestock began in the region in the late 1800s and has continued to varying degrees.

As of 2006, approximately 600,000 ha of converted farmland were enrolled in the CRP and had been planted to permanent cover in Washington State (U.S. Department of Agriculture 2007), mainly on nonirrigated land formerly planted to wheat. Conservation Reserve Program fields occurred in a range of landscape contexts, were planted with a variety of native and exotic plants, and had developed varying cover of native sagebrush. The first fields enrolled in the program (henceforth, 'Old CRP') were planted in the mid-1980s to exotic perennial grasses. Where these Old CRP fields were adjacent to stands of sagebrush, they frequently developed a shrub layer similar in height and cover to that of the surrounding shrubsteppe. Spread of sagebrush into CRP fields was enhanced by small patches of shallow, untillable soil that occurred in some fields and that retained shrubs and other native vegetation that provided additional seed sources. Fields without nearby sources of sagebrush seed remained largely as exotic grassland. Fields enrolled in the program after 1996 (henceforth, 'New CRP') were planted with a mix of native and exotic grasses and forbs, and in some areas, aridland shrubs (primarily big sagebrush [Artemisia tridentata]) to increase their value for wildlife. Some New CRP fields had developed varying cover of sagebrush up to 1 m in height by the beginning of our study.

METHODS

Study Design

We established 48 study sites in 3 habitat classes: Old CRP, New CRP, and Shrubsteppe (Fig. 1). Shrubsteppe sites were either fragments (areas of native habitat in a landscape fragmented by conversion to agricultural fields) or extensive patches of shrubsteppe. Study sites were grouped geographically into 8 clusters to minimize potential spatial effects and to increase sampling efficiency; each cluster included 1 extensive shrubsteppe site, 1 shrubsteppe fragment, and 4 CRP fields (2 Old and 2 New). All CRP fields occurred in areas that historically supported deep-soil shrubsteppe communities (Daubenmire 1970); most of the deep-soil shrubsteppe in this region has been converted to agriculture (Vander Haegen et al. 2000). We began by identifying appropriate, extensive patches of shrubsteppe with soils sufficiently deep to support a shrub layer dominated by big sagebrush. We then used data provided by the Farm Service Agency to identify former cropland enrolled in the CRP and to select suitable fields (those with established perennial vegetation) in the surrounding landscape. Because we did not select fields completely at random, our inference is restricted to native sites with shrub layers dominated by big sagebrush and to restored fields where plantings were successful. One of our sites, a CRP field, was grazed by livestock for a short time in autumn between field seasons.

Within each of the 48 study sites, we established a 25-ha (500×500 -m) plot, buffered by ≥ 50 m of similar habitat. We placed 4 100-m-radius point-count circles equidistant

(300 m between points) within the 25-ha plot; these circular plots were the focus of all data collection. We measured vegetation on each study site within $100 \text{-m}^2 (15 \text{-m} \times 6.7 \text{-m})$ sample plots located within each of the 4 100-m point-count circles. Each vegetation plot was anchored at a point a random distance and bearing from the survey point and positioned in a random direction. We completed sampling in June and July of 2003. We recorded all plant species observed within vegetation plots and visually estimated their cover as 1 of 9 values: 1) $\leq 1\%$; 2) >1-5%; 3) >5-15%; 4) >15-25%; 5) >25-35%; 6) >35-50%; 7) >50-75%; 8) >75-95%; and 9) >95%. We placed colored flags at set distances along the plot boundary to assist with cover estimates. We also estimated percent cover for general vegetation and substrate categories, including shrubs, perennial grasses, annual grasses, perennial forbs, all forbs (perennial and annual combined), rock and/or gravel, bare ground, biological soil crust, and litter. We recorded the maximum height for each category (nearest cm), other than bare ground, biological soil crust, and litter. We estimated visual obstruction (Robel et al. 1970) at 10 points along the perimeter of the plot, recording the lowest 10-cm segment visible on a pole when viewed at a distance of 4 m by an observer standing inside the plot (10 values were averaged to characterize the plot). All sampling was conducted by 2 professional botanists trained in visual estimation of cover. We used Analysis of Variance and Tukey's post hoc test to compare vegetation parameters among habitat types.

We derived 2 landscape variables for each study site using a geographic information system (ArcGIS). We used a raster



Figure 1. Study area in eastern Washington, USA, depicting major land-cover types and location of study sites. Land cover was derived from Landsat scenes dated 1993 and 1994 and from data provided by the U.S. Department of Agriculture.

land-cover data layer that identified native and converted land-cover types in eastern Washington (Jacobson and Snyder 2000) to estimate the percentage of the landscape in shrubsteppe habitat within a 1-km radius of each site center. Similarly, we used a polygon layer provided by the Farm Service Agency that depicted current CRP fields in eastern Washington to estimate proportion of CRP in the cropland component of the landscape within a 1-km radius of each site center. Our study sites were 25 ha and represented 8% of the 1-km-radius analysis area; the landscape metrics were designed to assess small-scale landscape composition around each site.

Abundance Estimates

We surveyed for birds at each site twice (May and Jun) in 2003, 2004, and 2005. We counted all birds seen or heard within 5 min of arriving at each point, along with their sex (if known), distance from the point (within 50 m, >50 but <100 m, or beyond 100 m), and behavior (singing, calling, silent, or flying over the circle). We surveyed only on mornings with no rain and low wind and between sunrise and 0900 hr. A crew of 8 biologists trained in bird identification conducted the surveys each year. Each biologist surveyed an equal number of study sites in each habitat type, minimizing the effects of potential observer bias.

We used the maximum number of birds counted on each site during the 2 counts as an estimate of the annual abundance of each species. This count was limited to birds seen or heard within 100 m of the survey point and excluded birds flying over the site, except for horned larks (Eremophila alpestris) engaged in aerial display. Although our survey design was insufficient to assess detection probability, analyses from later research in the same general study area using Program Distance (Buckland et al. 2001) identified similar detection probabilities in shrubsteppe and in CRP for 6 of the 8 species considered here (Schroeder and Vander Haegen 2014); data were insufficient to assess detection for the remaining 2 species. Estimates of effective detection radius ranged from 70 to 122 m for these 6 species, lending support to our choice of a 100-m cut-off for the present analysis (Schroeder and Vander Haegen 2014).

We fit models for 7 species with the largest sample size (>100 observations within 100 m) and for 2 species groups: grassland birds (grasshopper sparrow [Ammodramus savannarum], horned lark, Savannah sparrow [Passerculus sandwichensis], and western meadowlark [Sturnella neglecta]) and shrubland birds (Brewer's sparrow [Spizella breweri], sagebrush sparrow [Artemisiospiza nevadensis], and sage thrasher [Oreoscoptes montanus]). We did not include vesper sparrow [Pooecetes gramineus] in either group for analysis because of their more generalist habitat affinities that have them associated with grasslands in some areas and woody vegetation in others (Vander Haegen et al. 2000, Jones and Cornely 2002), although for purposes of discussion we include them with shrubland birds.

We used linear models and the SAS (Version 9.1.3) NLMIXED procedure to examine the relationship between site and landscape variables and the abundance of each

species and species group. Models included Site as a random effect, treating yearly observations from a single site as repeated measures. We assumed that the species-specific abundance followed the Poisson, Negative binomial, Zero-inflated Poisson, or Zero-inflated Negative Binomial models. We used presence of shrubs on the site for the logistic component of the Zero-inflated models because of its potentially large effect on suitability of sites for shrub-nesting species. We fit the global models (described below) under the 4 distributional assumptions for each species or species group and selected the model with the lowest Akaike's Information Criterion (adjusted for small sample sizes; AIC_c). We examined plots of observed versus predicted values and residuals using the best-fit model for each species to look for indications of poorly fitting models.

We developed 7 candidate models using uncorrelated (|r| < 0.6) covariates describing landscape, vegetation, and CRP management. A landscape model contained the 2 parameters derived via geographic information system quantifying shrubsteppe and CRP in the surrounding landscape. A vegetation model included percent cover of shrubs, perennial grasses, perennial forbs, all forbs (perennial and annual), height of perennial grass, and visual obstruction. A management model represented management history of the site under the CRP and differentiated sites in Old CRP, New CRP, and Shrubsteppe. The complete model set included combinations of these models and a Global model with all 3. Shrub cover and shrub height were highly correlated; we chose to include only shrub cover in appropriate models. We tested for 2-way interactions between landscape and management variables, between landscape and vegetation variables, and between management and vegetation variables. We used the top model (lowest AIC_c) for each of the 2 species groups to predict the abundance of grassland birds and shrubland birds with increasing shrub cover within the range of shrub cover values measured on our sites. We modeled this relationship individually for each habitat type, setting all other parameters to their group means.

Reproductive Success

Nest survival.—We searched for nests in 16 CRP sites (8 Old, 8 New) that had the greatest amount of shrubsteppe in the surrounding landscape (>18% within 1 km) and in the 8 extensive shrubsteppe sites. We chose not to include sites in highly fragmented landscapes in order to maximize our opportunity to test for management effects; previous research in Washington's shrubsteppe documented a negative effect of landscape fragmentation on nesting success of several shrubsteppe passerines (Vander Haegen 2007). We located nests by following behavioral cues of color-banded birds during semiweekly observation bouts (see Seasonal reproductive success). We also found nests opportunistically while conducting point counts, mist netting, and vegetation sampling on the plots. Total effort expended locating nests was similar among years. We placed a single flag $\geq 8 \text{ m}$ from nests to mark their location and revisited nests every 2-4 days until they fledged or failed. We noted number of eggs and

nestlings and presence of brown-headed cowbird (*Molothrus ater*) eggs and chicks at visits.

We considered nests as depredated when eggs or young nestlings disappeared from the nest or when empty nests appeared damaged or torn, as if by a predator. We considered a nest to have fledged when 1) the nest was empty and we found feces on the rim of the nest or immediately adjacent to the nest, 2) we saw fledglings near the nest or adults were seen nearby carrying food and/or scolding, or 3) the nest was empty and the median date between the last nest check during which the nest was active and the final nest check when the nest was empty was within 2 days of the predicted fledging date (Martin et al. 1997). Because predators may depredate nests with young near fledging age without leaving sign, we acknowledge that our nest survival estimates may be biased slightly high (Pietz et al. 2012). We defined successful nests as those that fledged ≥ 1 young and we used the last count of nestlings before fledging as an estimate of the number of fledglings produced. Mean values for number of eggs laid in complete clutches and number of fledglings produced from successful nests can be found in the Supporting Information (available online).

We sampled the vegetation at each nest site after the nest had fledged or failed. We used rectangular plots centered on the nest and formed by 5-m-long transects extending in the 4 cardinal directions. We estimated visually the percent cover of each of the following components in the resulting 5×5 -m quadrants: shrubs, perennial grasses, annual grasses, forbs, rock, and open ground. We estimated visual obstruction using methods described above at points 1, 3, and 5 m from the nest along each transect and directly at the nest (16 readings total that were averaged to characterize the nest site). We measured the height of herbaceous vegetation at the point where each visual obstruction measurement was taken and took the mean of these values. We measured the height of the shrub that was closest to the plot center in each of the 4 quadrants and averaged these to derive a mean shrub height for the nest site. We estimated how well the nest was hidden from visual predators by visualizing a flat disc 25 cm in diameter placed at the nest and estimating the percentage of that disk that would be obscured by vegetation when viewed from directly above and from the side in the 4 cardinal directions.

Seasonal reproductive success.—We obtained information on males of 2 focal species to gain further insight on reproductive success (limited to the same plots used for nest searching). We captured Brewer's sparrow and Savannah sparrow males using song play-back and mist nets, and we banded them with unique combinations of color bands and U.S. Fish and Wildlife Service metal bands. We attempted to band the male of each species closest to each point-count center on each plot; in some cases, a female associating with the target male also was captured and banded. If a banded male was not relocated on 2 subsequent visits we attempted to capture and band another male. We visited focal males twice each week, spending a minimum of 30 min on each territory per visit documenting behaviors that would indicate the male's reproductive status, such as

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associating with a female (indicating paired status), feeding fledglings (indicating successful reproduction), or feeding fledglings from a second successful nest (indicating successful renesting; Vickery et al. 1992, Vander Haegen 2007). We limited our analysis to males that were visited ≥ 10 times (Vander Haegen 2007).

We estimated seasonal reproductive success for Brewer's sparrows and Savannah sparrows by averaging the number of young fledged by focal pairs each year in Old CRP, New CRP, and in Shrubsteppe. We included only pairs that were tracked sufficiently that we were confident all nesting attempts were documented. In 21% of cases, nests were not located but the focal male or focal pair was found feeding fledglings; when an accurate count of fledged young was unavailable, we substituted the mean value for that species for the relevant year and habitat type for the missing value. In several cases only failed nests were observed for individual pairs and these pairs were attributed with a seasonal reproductive success of zero.

Statistical analysis.—We used the logistic-exposure method of Shaffer (2004) to examine the influence of management, vegetation, nest position, and temporal variables on the fates of individual nests. The data set used for analysis of nest success included all nests where eggs were laid and that could be tracked sufficiently to their conclusion (99% of all nests found). We limited the analysis to nests that were either successful or that failed because of predation (>96% of all nests). We excluded nests that were parasitized by brownheaded cowbirds (<3% for any species).

We developed a set of 9 a priori models using uncorrelated (|r| < 0.6) covariates describing CRP management, vegetation structure, and characteristics of the nest. A management model included identical parameters to those used in the abundance analysis. A site-vegetation model included variables measured in vegetation plots positioned to characterize the study site: percent cover of shrubs, percent cover of perennial grasses, and percent cover of all forbs. A nest-vegetation model included parameters measured at each specific nest site: percent cover of shrubs, percent cover of perennial grasses, percent cover of all forbs, height of herbaceous vegetation, shrub height, and visual obstruction. A nest position model included 2 variables: nest concealment and nest height (the latter variable excluded in models for ground-nesting species). We combined these variable sets to create 5 additional models: Management + Site vegetation, Management + Nest vegetation, Site vegetation + Nest position, Nest vegetation + Nest position, and a Global model with all variables. We tested for 2-way interactions between year and habitat, year and each vegetation variable, and habitat and each vegetation variable. To examine the potential effects of temporal variables we added 2 variables to the best-fitting model for each species and compared AIC_c values for evidence of improved model fit: Julian (equaling the last day in each exposure period [where 1 Jan = day 1]) and nest age (in days, where day 1 was the estimated first day of laying). We estimated the first day of laying by backcalculating from known or estimate fledging dates, hatch dates, or from the number of eggs laid for nests found before

the clutch was completed. If a nest was found during incubation but depredated before hatching, we assigned a date back-calculated from the mid-point of the known incubation period for that species.

For each species, we tested the global model for goodnessof-fit using the Hosmer and Lemeshow (2000) goodness-offit test (all tests confirmed adequate model fit [P > 0.125]). We used diagnostics within the GENMOD procedure (SAS Institute, Cary, North Carolina) to examine standardized deviance residuals for the global model, where large values (≥ 3) would suggest outliers. We used the REG procedure (SAS Institute) to examine multicollinearity of continuous variables in the global model (Allison 1999). We used code developed by Shaffer (2004) for the GENMOD procedure to fit models for each species and to calculate AIC_c and Akaike weights (w) for the full model set. We calculated odds ratios from parameter estimates and confidence intervals (CI) based on unconditional standard errors for the subset of models containing each variable (Burnham and Anderson 2002). We used the package MuMIn in the R programing language (R Development Core Team 2011) to calculate habitat-specific daily survival rates (DSRs) for each species using model-averaging.

For both bird abundance and nesting success we used an information-theoretic approach (Burnham and Anderson 2002) to rank the relative importance of the models and to identify meaningful covariates. We considered models with ΔAIC_c values ≤ 2 as competing with the minimum AIC model and comprising what we refer to as the top model set (Burnham and Anderson 2002). To account for model selection uncertainty, we calculated model-averaged coefficients and unconditional variance estimates using model weights adjusted by the total weights from the selected models (Burnham and Anderson 2002). We calculated relative variable importance (RVI) by summing the weights across models that included that variable (Burnham and Anderson 2002).

We took different approaches to summarizing the results of model selection and interpretation of coefficients for the abundance versus nest-success data sets that reflected the different goals of these separate analyses. Our assessment of abundance focused on the species groups of interest (shrubland and grassland birds); here, we looked for concurrence in top models and in the strongest (CI not including zero) explanatory variables identified via modelaveraging. We also looked for consistency in the direction of parameter estimates across species within these groups. Our analysis of reproductive success focused on individual species, answering the primary question of whether CRP was suitable as nesting habitat. We also examined odds ratios to quantify the effects of specific variables on daily survival rate of nests. Parameter estimates and CIs for all explanatory variables can be found in the Supporting Information available online.

RESULTS

Vegetation Characteristics

Shrubsteppe sites surveyed in the study were sagebrushbunchgrass communities (A. tridentata, A. rigida) with a grass component that included Sandberg bluegrass (Poa secunda), bluebunch wheatgrass (Pseudoroegneria spicata), needle and thread grass (Hesperostipa comata), and Idaho fescue (Festuca idahoensis), and a diverse forb community that included lupin (Lupinus spp.), fleabane (Erigeron spp.), and desert parsley (Lomatium spp.). Grasses were the dominant vegetation cover on all sites, with mean cover values similar among habitat types ($F_{2,45} = 0.77$, P = 0.470; Table 1). Old CRP was predominantly exotic perennial grasses including crested wheatgrass (Agropyron cristatum), tall wheatgrass (Thinopyrom ponticum), and intermediate wheatgrass (T. intermedium); whereas New CRP was dominated by native grasses or cultivars (primarily Poa ampla and P. spicata). Mean height of perennial grass differed among habitat types ($F_{2,45} = 8.9$, P < 0.001) and was greatest in New CRP (Table 1). Percent cover of perennial forbs ($F_{2,45} = 0.70$, P = 0.502) and of all forbs ($F_{2,45} = 0.82$, P = 0.449) was similar among site types (Table 1). Dominant forbs planted in CRP were alfalfa (Medicago sativa) and common varrow (Achillea millefolium); other forbs that were relatively common included tall annual willowherb (Epilobium brachycarpum), shaggy fleabane (Erigeron pumilus), and yellow salsify (Tragopogon dubius). Percent cover of shrubs was greater in Shrubsteppe than in either CRP type ($F_{2,45} = 23.9$, P < 0.001; Table 1). Because of large variances, Old and New CRP sites had statistically similar shrub cover with big sagebrush and gray rabbitbrush (Ericameria nauseosa) most common (Table 1). Mean height of shrubs differed across habitat types ($F_{2,45} = 17.4$, P < 0.001) and was greatest in Shrubsteppe (Table 1).

Table 1. Vegetation characteristics of study plots in native shrubsteppe and in Conservation Reserve Program fields (CRP) planted with exotic bunchgrasses (Old CRP) and with a mix of exotic and native bunchgrasses (New CRP) in eastern Washington, USA, 2003–2005 (n = 16 for each of the 3 site types). Means followed by the same letter within rows were similar (P > 0.050).

	Shrubsteppe		Old CRP		New CRP	
Variable	$ar{m{x}}$	SE	\bar{x}	SE	\bar{x}	SE
Shrubs (% cover)	15.79 ^A	2.08	5.00 ^B	1.98	1.98 ^B	1.16
Shrub height (cm)	102.95^{A}	4.52	64.74 ^B	10.55	29.45 ^C	10.08
Perennial grass (% cover)	69.17 ^A	2.07	75.25 ^A	3.83	71.92 ^A	5.54
Perennial grass height (cm)	42.49 ^A	2.44	45.33 ^A	1.75	56.81 ^B	3.24
All forbs (% cover)	11.64 ^A	1.69	16.81^{A}	3.05	18.58^{A}	4.25
Perennial forbs (% cover)	4.24 ^A	0.66	6.34 ^A	2.88	3.02^{A}	0.66
Visual obstruction (cm)	11.13 ^A	1.47	5.37 ^B	0.74	7.94 ^{AB}	1.02

Mean visual obstruction differed among habitat types $(F_{2,45} = 6.7, P = 0.003)$ and was greatest in Shrubsteppe and in New CRP (Table 1).

Bird Abundance

We counted 2,309 birds that fit our criteria during pointcount surveys in 2003, 2,462 birds in 2004, and 1,939 birds in 2005. Cumulative counts in each of the 3 habitat types were similar and exceeded 2,200 individual observations over the 3 years. The prominent species, however, varied among habitat types with grassland species clearly the most abundant in CRP habitats and shrubland species most abundant in Shrubsteppe. Savannah sparrow was the most numerous species in New CRP sites, followed by horned lark and grasshopper sparrow; these 3 species also dominated Old CRP sites (Fig. 2). Brewer's sparrow was the most numerous species in shrubsteppe, followed by vesper sparrow and western meadowlark (Fig. 2).

Brewer's sparrows, sagebrush sparrows, sage thrashers, and vesper sparrows all occurred in CRP (Fig. 2), but mainly on sites that contained mature sagebrush. Of the sagebrush obligates, Brewer's sparrows made most use of CRP and occurred in 19 of 32 CRP sites; sage thrashers occurred in 5 CRP sites; and sagebrush sparrows occurred in 1 CRP site. Most CRP sites had little or no shrub cover. When we examined the 5 Old CRP sites where shrub cover exceeded 5%, mean abundance values for Brewer's sparrow (2.16, SE = 0.26) and for vesper sparrow (1.77, SE = 0.24) were similar to those in shrubsteppe (2.27, SE = 0.36 and 1.41, SE = 0.18 for these 2 species, respectively); for sage thrashers, mean abundance in these 5 Old CRP fields (0.25, SE = 0.16) approached that in shrubsteppe (0.54, SE = 0.11).

Models that included landscape variables were in the top model set ($\leq 2 \Delta AIC_c$) for 3 species and comprised the entire top model set for western meadowlark (Table 2). For western meadowlark, the Landscape and Landscape + Management models held nearly all of the model weight (96%), and the effect of percent shrubsteppe in the landscape was strongly positive (Table 3). Proportion of CRP in the cropland component of the landscape was not a strong predictor for any species or species group.

Models that included management variables were in the top model set for all species except western meadowlark and comprised the entire top model set for the Shrubland and Grassland bird groups, vesper sparrow, and grasshopper sparrow (Table 2). Predicted abundance of sage thrashers showed positive response to Shrubsteppe over CRP



Figure 2. Mean abundance (no. counted/survey) of shrubland and grassland birds on sites in native shrubsteppe and in Conservation Reserve Program lands (CRP) planted with exotic bunchgrasses (Old CRP) and with a mix of exotic and native bunchgrasses (New CRP) in eastern Washington, USA (n = 16 for each of the 3 types). Means represent the maximum individuals counted on annual 100-m-radius point-count surveys across 3 years (2003–2005). Stems indicate 95% confidence interval.

Table 2. Models of predicted species abundance for shrubland birds and grassland birds in native shrubsteppe and in Conservation Reserve Program fields in
eastern Washington, USA, showing Akaike's Information Criterion (AI \hat{C}_c), differences in AI \hat{C}_c values from the top model (Δ AI \hat{C}_c), and model weight (ω).
All models with Δ AIC, values within 4 units of the best model are shown.

Group and species	Model ^a	AIC	ΔAIC_{c}	w
Shrubland birds				
Brewer's sparrow	Vegetation	604.1	0.0	0.428
I.	Management+Vegetation	604.6	0.5	0.333
	Landscape+Vegetation	606.9	2.8	0.105
Sage thrasher	Management	235.3	0.0	0.408
C	Landscape	235.8	0.5	0.318
	Landscape+Management	237.0	1.7	0.174
Vesper sparrow	Management+Vegetation	625.6	0.0	0.899
Shrubland bird group ^b	Management+Vegetation	639.4	0.0	0.638
	Global	642.6	3.2	0.129
	Landscape+Vegetation	642.6	3.2	0.129
	Vegetation	643.1	3.7	0.100
Grassland birds	-			
Grasshopper sparrow	Management+Vegetation	605.2	0.0	0.822
	Global	608.5	3.3	0.158
Savannah sparrow	Vegetation	738.9	0.0	0.477
-	Management+Vegetation	739.5	0.6	0.353
	Global	742.1	3.2	0.096
Horned lark	Management+Vegetation	778.2	0.0	0.285
	Landscape+Vegetation	778.3	0.1	0.271
	Management	779.0	0.8	0.191
	Landscape	780.5	2.3	0.090
	Vegetation	781.1	2.9	0.067
	Global	781.3	3.1	0.061
Western meadowlark	Landscape	624.6	0.0	0.717
	Landscape+Management	626.8	2.2	0.239
Grassland bird group ^c	Management+Vegetation	1,011.1	0.0	0.592
~ .	Vegetation	1,013.7	2.6	0.161
	Management	1,014.5	3.4	0.108

^a Models are defined in the text. Based on AIC_c values for the global model, Poisson models provided the best fit for Brewer's sparrow, sage thrasher, and vesper sparrow; whereas, negative binomial models were best for grasshopper sparrow, horned lark, Savannah sparrow, western meadowlark, and both the grassland and shrubland bird groups.

^b Shrubland bird group: Brewer's sparrow, sagebrush sparrow, and sage thrasher.

^c Grassland bird group: grasshopper sparrow, Savannah sparrow, horned lark, and western meadowlark.

Table 3. Model-averaged parameter estimates, lower (LCI) and upper (UCI) 95% confidence intervals, and Relative Variable Importance (RVI) for variables in models of species abundance in Conservation Reserve Program fields (CRP) and in native shrubsteppe in eastern Washington, USA, 2003–2005. For species that only had parameter estimates whose 95% Confidence Intervals overlapped zero, we report results for the variables with the highest RVI.

Species and group	Variable	Parameter Estimate	LCI	UCI	RVI
Brewer's sparrow	Shrub cover	0.122	0.032	0.212	0.907
Sage thrasher	Habitat ^a	1.374	-0.305	3.053	0.628
Vesper sparrow	Shrub cover in Old CRP ^b	0.096	0.032	0.161	0.980
	Shrub cover in New CRP ^b	0.200	0.095	0.305	0.980
	Forb cover	0.033	0.061	0.005	0.980
Shrubland bird group ^e	Shrub cover	0.120	0.065	0.175	0.997
Grasshopper sparrow	Shrub cover	-0.076	-0.111	-0.041	0.999
	Perennial forb cover	-0.030	-0.059	-0.001	0.999
	Habitat_S/N ^a	-1.450	-2.092	-0.808	0.981
Savannah sparrow	Shrub cover	-0.115	-0.195	-0.036	0.975
Horned lark	Shrub cover	-0.017	-0.038	0.004	0.684
	Perennial grass cover	-0.011	-0.026	0.003	0.684
Western meadowlark	Shrubsteppe in landscape ^d	0.012	0.006	0.018	0.979
Grassland bird group ^e	Shrub cover	-0.024	-0.041	-0.006	0.875

^a Habitat indicates abundance in Shrubsteppe compared with CRP; S/N indicates abundance in Shrubsteppe compared with New CRP.

^b Indicates effect of shrub cover in the designated habitat type.

^c Shrubland bird group: Brewer's sparrow, sagebrush sparrow, and sage thrasher.

^d Proportion of Shrubsteppe (all non-converted lands) within 1-km radius of the survey point.

^e Grassland bird group: grasshopper sparrow, Savannah sparrow, horned lark, and western meadowlark.

(Table 3), and predicted abundance of grasshopper sparrow was greater for New CRP than for Shrubsteppe (Table 3).

Models that included vegetation variables occurred in the top model set for all species except sage thrasher and western meadowlark and comprised the entire top model set for the Shrubland bird group, the Grassland bird group, Brewer's sparrow, vesper sparrow, grasshopper sparrow, and Savannah sparrow (Table 2). Shrub cover was consistently the strongest variable in the vegetation set and was positive for Brewer's sparrow and the Shrubland bird group and negative for grasshopper sparrow, Savannah sparrow, horned lark, and the Grassland bird group (Table 3; Fig. 3). There was a significant interaction between habitat and shrub cover for vesper sparrow; effect of shrub cover on predicted abundance was strongly positive for both CRP types but slightly negative for Shrubsteppe (Table 3). Percent cover of forbs had a positive effect on predicted abundance of vesper sparrows and percent cover of perennial forbs had a negative effect on predicted abundance of grasshopper sparrows (Table 3).

Nest Survival

We located and monitored 1,377 nests over the course of the study. We developed models of nest survival for Brewer's sparrow (n = 612 nests), sage thrasher (n = 81), vesper sparrow (n = 181), Savannah sparrow (n = 201), horned lark (n = 72), and western meadowlark (n = 45). Predation was the dominant cause of nest loss (31% of all nests were depredated), followed by abandonment (3.6%). Rate of parasitism by brown-headed cowbirds was low: 2.9% for Savannah sparrow, 1.5% for Brewer's sparrow, 0.6% for vesper sparrow, and undetected for other species.

Management was in the top model set for 3 of the 6 species (Table 4) and the parameter estimate for Savannah sparrow indicated a positive relationship for CRP compared with shrubsteppe (Table 5). Estimated DSRs derived through model-averaging were equal or greater for nests in CRP compared with nests in shrubsteppe for all 5 species with sample size sufficient for analysis (Table 6). Confidence intervals for the 3 habitat types overlapped for all species (Table 6). Models that included temporal variables were not competitive ($\Delta AIC_c > 2$) with the top model for any species.

Brewer's sparrow.—We monitored Brewer's sparrow nests through 2,385 intervals (323 in 2003, 813 in 2004, and 1,249 in 2005). There was a significant interaction between Management and both grass cover and forb cover at the site level and grass cover at the nest level. We revised the model set for Brewer's sparrow to include these interaction terms when vegetation variables were present. Management + Site vegetation was the dominant model, with a weight of 0.68 (Table 4). Grass cover at the site level had a positive effect on DSR in Shrubsteppe habitat but not in CRP (Table 5).

Sage thrasher.—We monitored sage thrasher nests through 395 intervals (37 in 2003, 91 in 2004, and 268 in 2005). We combined nests across CRP classes because of low sample size in New CRP. Grass cover at the nest was correlated with other variables in the sage thrasher data set, so we removed this variable from all models. Nest vegetation + Nest position was the best model, with 0.92 of the model weight (Table 4), and we derived odds ratios for parameters from this model. Forb cover, herbaceous height, and visual obstruction at the nest all were negatively associated with DSR, whereas both nest height and nest cover were



Figure 3. Predicted abundance (no./ha) of shrubland and grassland birds as a function of shrub cover on sites in native shrubsteppe and in Conservation Reserve Program lands (CRP) planted with exotic bunchgrasses (Old CRP) and with a mix of exotic and native bunchgrasses (New CRP) in eastern Washington, USA. Abundance estimates were derived from best-fitting models for the shrubland and grassland bird groups by selecting for habitat type (Shrubsteppe, Old CRP, New CRP) and setting other variables to their group means.

Table 4. Models of daily nest survival for shrubland bird and grassland birds in native shrubsteppe and in Conservation Reserve Program fields in eastern Washington, USA, 2003–2005, showing Akaike's Information Criterion (AIC_c), differences in AIC_c values from the top model (Δ AIC_c), and model weight (w). All models with Δ AIC_c values within 4 units of the best model are shown.

Species	Model ^a	AIC _c	ΔAIC_{c}	w
Brewer's sparrow	Management+Site vegetation	1,269.1	0.0	0.683
	Site vegetation+Nest position	1,272.5	3.3	0.129
	Management	1,272.5	3.4	0.126
Sage thrasher	Nest vegetation+Nest position	169.5	0.0	0.916
Vesper sparrow	Nest position	380.6	0.0	0.377
	Site vegetation	381.1	0.5	0.288
	Site vegetation+Nest position	382.7	2.1	0.135
	Management	383.1	2.5	0.110
	Management+Site vegetation	384.4	3.8	0.057
Savannah sparrow	Management+Site vegetation	295.7	0.0	0.435
	Management+Nest vegetation	297.3	1.5	0.199
	Global	297.4	1.7	0.184
	Management	298.3	2.6	0.120
Horned lark	Nest position	153.6	0.0	0.656
	Management	156.1	2.5	0.188
Western meadowlark	Nest vegetation	102.4	0.0	0.262
	Management+Nest vegetation	102.8	0.4	0.220
	Nest position	103.6	1.1	0.144
	Management	103.7	1.2	0.141
	Nest vegetation+Nest position	104.5	2.1	0.093
	Management+Site vegetation	104.7	2.3	0.083

^a Models are defined in the text.

positively associated with DSR (Table 5). The Management variable had very low RVI (<0.06).

Vesper sparrow.—We monitored vesper sparrow nests through 671 intervals (178 in 2003, 273 in 2004, and 220 in 2005). Nest position was the top-ranked model, with 38% of the model weight; other models in the top set included Site vegetation and Nest position (Table 4). Cover of perennial grass at the site level was positively associated with DSR (Table 5). The Management variable for vesper sparrow had low RVI (0.17).

Horned lark.—We monitored horned lark nests through 252 intervals (83 in 2003, 118 in 2004, and 51 in 2005).

There were insufficient nests in Shrubsteppe habitat to model DSR, so we developed models based only on nests in CRP. Nest Position was the dominant model for horned lark, with a weight of 0.66 (Table 4); DSR was positively associated with nest cover (Table 5). The Management variable for horned lark had low RVI (0.22).

Savannah sparrow.—We monitored Savannah sparrow nests through 505 intervals (107 in 2003, 273 in 2004, and 125 in 2005). Management + Site vegetation was the top-ranked model, with 44% of the model weight; other models in the top model set included Nest vegetation and Nest position variables (Table 4). Daily survival rate reflected a

Table 5. Odds ratios, 95% Confidence intervals (LCI, UCI), and relative variable importance (RVI) for variables in models of daily survival rates of nests for shrubland birds and grassland birds in native shrubsteppe and in Conservation Reserve Program fields (CRP) in eastern Washington, USA, 2003–2005. For species that only had parameter estimates whose 95% Confidence Intervals included 1, we report results for the variables with the highest RVI.

Species	Variable	Odds ratio	LCI	UCI	RVI
Brewer's sparrow	Grass cover in shrubsteppe ^a	1.039	1.005	1.073	0.812
Sage thrasher	Forb cover at nest ^b	0.839	0.769	0.914	0.947
0	Visual obstruction at nest	0.948	0.917	0.980	0.947
	Herb height at nest	0.972	0.948	0.995	0.947
	Cover at nest	1.047	1.016	1.078	0.778
	Nest height	1.039	1.009	1.069	0.778
Vesper sparrow	Grass cover	1.019	1.000	1.038	0.482
Horned lark	Nest cover	1.024	1.004	1.045	0.748
Savannah sparrow	Habitat_N/S ^c	5.758	1.072	30.929	0.939
-	Habitat_O/S	11.052	1.335	91.517	0.939
	Shrub cover	1.097	1.011	1.190	0.639
	Herb height at nest	1.027	1.007	1.048	0.426
Western meadowlark	Visual obstruction at nest	1.079	0.997	1.168	0.589

^a Indicates effect of grass cover in Shrubsteppe habitat type.

^b Variables measured at the nest; other variables were measured in plots that characterized the general site.

^c N/S indicates daily survival rate in New CRP compared with shrubsteppe; O/S indicates daily survival rate in Old CRP compared with Shrubsteppe.

Table 6. Daily survival rates (mean, lower [LCL] and upper [UCL] 95% confidence intervals, no. of nests) for nests in native shrubsteppe and in Conservation Reserve Program fields (CRP) planted with exotic bunchgrasses (Old CRP) and with a mix of exotic and native bunchgrasses (New CRP) in eastern Washington, USA, 2003–2005.

Species	Habitat class	\bar{x}	LCL	UCL	n
Brewer's sparrow	New CRP	0.982	0.944	0.994	81
1	Old CRP	0.978	0.968	0.985	248
	Shrubsteppe	0.973	0.966	0.980	283
Sage thrasher	CRP ^a	0.991	0.981	0.996	43
	Shrubsteppe	0.992	0.980	0.996	38
Vesper sparrow	New CRP	0.974	0.963	0.982	39
	Old CRP	0.975	0.964	0.982	55
	Shrubsteppe	0.974	0.964	0.981	87
Horned lark ^b	New CRP	0.968	0.943	0.983	21
	Old CRP	0.965	0.947	0.977	51
Savannah sparrow	New CRP	0.978	0.962	0.987	84
	Old CRP	0.988	0.971	0.995	86
	Shrubsteppe	0.895	0.593	0.980	31
Western meadowlark	CRP ^a	0.972	0.920	0.990	19
	Shrubsteppe	0.965	0.931	0.982	26

^a Nests in Old CRP and New CRP combined.

^b No. of nests in Shrubsteppe (n = 10) was insufficient for survival rate estimation.

strong influence of Management with both CRP types strongly positive over Shrubsteppe (Table 5). Shrub cover at the site level and herbaceous height at the nest also were associated positively with DSR (Table 5).

Western meadowlark.—We monitored western meadowlark nests through 136 intervals (42 in 2003, 57 in 2004, and 37 in 2005). We found few nests in New CRP, so we combined nests between CRP classes. Shrub cover was correlated with other variables in the meadowlark data set, so we removed this variable from all models. Six models were in the top model set for western meadowlark, with no single model strongly dominant (Table 4); however, only Management and Nest vegetation variables had high RVI (0.46 and 0.59, respectively). Visual obstruction at the nest was positively associated with DSR and had the highest RVI though the parameter estimate had a 95% CI that included 1 (Table 5).

Seasonal Reproductive Success

We color-banded and tracked 112 male Brewer's sparrows over 3 years of the study (56 in Shrubsteppe; 42 in Old CRP; 14 in New CRP). Pairing success was high in all habitat types and averaged 93.7% (SE = 0.01; $\chi^2 = 0.26$, P = 0.870). We documented seasonal reproductive success (no. of young/ nesting pair in the population) for 81 focal pairs (37 in Shrubsteppe, 33 in Old CRP, 11 in New CRP). Sample size ranged from 5 to 18 pairs for each of the 8 Year and Habitat classes considered. Seasonal reproductive success of Brewer's sparrows in Old and in New CRP was similar and within the range of values documented for shrubsteppe sites (Fig. 4). Seasonal reproductive success of focal pairs in Shrubsteppe was more variable among years than for pairs in CRP and attained a maximum value of 4.3 in 2005 as a result of frequent double-brooding (Fig. 4). Although DSR of nests was somewhat lower in Shrubsteppe, pairs maintained high seasonal reproductive success through renesting following nest loss and by raising multiple broods; we documented

double broods for 7 males in shrubsteppe compared with 1 in CRP.

We color-banded and tracked 122 male Savannah sparrows over 3 years of the study (16 in Shrubsteppe; 41 in Old CRP; 65 in New CRP). Pairing success was 81.5% in New CRP, 87.8 in Old CRP, and 87.5 in Shrubsteppe ($\chi^2 = 0.88$, P = 0.440). We documented seasonal reproductive success for 58 focal pairs (10 in Shrubsteppe; 24 in Old CRP; 24 in New CRP). Sample size ranged from 4 to 12 pairs for each of the 7 Year and Habitat classes considered. Seasonal reproductive success was similar in Old and New CRP, with a mean of 3.7 young fledged/pair (Fig. 4). Despite considerably lower DSR for nests in Shrubsteppe, focal pairs in native habitat attained seasonal reproductive success close to that of pairs in CRP in 1 of 2 years through a combination of renesting after nest failure and double-brooding. We documented double broods for 2 males in Shrubsteppe, 3 in New CRP, and 3 in Old CRP.

DISCUSSION

The impetus for this study was the continuing loss and fragmentation of shrubsteppe communities in the Intermountain West and the concomitant decline in populations of some shrubland and grassland birds (Dobkin and Sauder 2004, Sauer et al. 2005). Studies in the prairie regions of the Midwest suggest that large-scale grassland restoration provided by the CRP is having positive effects on grassland bird populations (Haroldson et al. 2006, Niemuth et al. 2007, Nielson et al. 2008, Herkert 2009); our data suggest that CRP could have similar benefits for shrubland and grassland birds in the Intermountain West. Grassland birds were most abundant on our CRP plots and appear to be the main beneficiaries of these new perennial grasslands. Shrubland birds, in contrast, were most closely associated with native sagebrush-steppe and the shrubs that are a prominent component of this system. Where shrubland birds used CRP, they were most often observed in older stands



Figure 4. Seasonal reproductive success (young produced/breeding pair [mean \pm 95% CI]) and daily nest survival for focal Brewer's sparrows and Savannah sparrows in native shrubsteppe and Conservation Reserve Program lands (CRP) planted with exotic bunchgrasses (Old CRP) and with a mix of exotic and native bunchgrasses (New CRP), eastern Washington, USA, for years 2003, 2004, and 2005. Each point equals 1 year; not all years are represented for each species and habitat class.

where mature sagebrush was more common. Shrubcover appeared to play a more important role than management (planting of native vs. exotic grasses) or landscape in affecting abundance of most species in our study. Previous studies also have reported decreasing abundance of grasshopper sparrows (Earnst and Holmes 2012) and Savannah sparrows (Winter et al. 2006, Earnst and Holmes 2012) and increasing abundance of sagebrush-obligate passerines (Wiens and Rotenberry 1981, Knick and Rotenberry 1995, Vander Haegen et al. 2000, Earnst and Holmes 2012) with increasing shrub cover. These strong relationships with dominant vegetation life forms follow the template presented by Rotenberry and Wiens (1980) for grassland and shrubsteppe bird communities at a regional scale.

Bird Abundance in CRP Grasslands

Perennial grasslands that had been in the CRP the longest had the greatest opportunity to provide mature sagebrush for foraging and nesting structure and their proximity to extant shrubsteppe as a source of sagebrush seed was largely responsible for development of this important structural component. Some CRP fields that had been planted in the mid-1980s had developed shrub layers virtually indistinguishable from neighboring shrubsteppe. Resiliency of some shrubland birds to alteration of their habitat has been documented previously in shrubsteppe, where removal of sagebrush from native habitat and subsequent planting of crested wheatgrass was a common technique for increasing livestock forage (Braun et al. 1976, Young et al. 1979). Sites converted to crested wheatgrass and lacking a shrub component typically had few or no shrubland birds, whereas several species returned to these altered rangelands when sites were recolonized by sagebrush (Reynolds and Trost 1981, McAdoo et al. 1989). Some of the more recently planted CRP in our study included sagebrush in the seed mix, hastening development of a shrub layer, and allowing development of a shrub component distant from native seed sources. Lower use of these New CRP fields by shrubland

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birds in our study likely was related to the small stature of young sagebrush that had not attained heights suitable for nesting by some species. As sagebrush on these sites matures, we would expect to see increased use by sage thrashers, sagebrush sparrows, greater sage-grouse, and other wildlife, such as pygmy rabbits (*Brachylagus idahoensis*) that depend on tall sagebrush (Green and Flinders 1980).

Although landscape parameters were not strongly associated with abundance for most species in our study, there are clear benefits to encouraging CRP enrollment and other types of grassland restoration near extant shrubsteppe. Restored grasslands extend the nontilled component of the landscape, providing larger blocks of unfragmented habitat for area-sensitive species such as sagebrush sparrows that are excluded from small, isolated patches (Knick and Rotenberry 1995, Vander Haegen et al. 2000). Moreover, as restored grasslands join with extant shrubsteppe to expand the permanent cover in an area, this developing landscape may increase productivity for a number of shrubsteppe passerines that are subject to deleterious effects of fragmentation by cropland (Vander Haegen 2007). Western meadowlarks also were more abundant as the proportion of shrubsteppe increased on the landscape in our study, suggesting that this species would benefit from CRP near extant shrubsteppe. Proximity of native shrubsteppe also serves as a seed source for sagebrush and other native species, particularly forbs.

Numerous studies have documented greater abundance of grassland birds in CRP compared with the cropland that it replaced (e.g., Johnson and Schwartz 1993, King and Savidge 1995, Best et al. 1997); however, few studies have compared bird communities in these new perennial grasslands with those in the native vegetation community that preceded cultivation. Generally, grassland birds were found in similar or greater numbers in CRP compared with nearby native prairie (Fletcher and Koford 2002, Chapman et al. 2004, Lloyd and Martin 2005, Ribic et al. 2009). Grassland birds in our study area were more abundant in CRP than in Shrubsteppe, with the exception of western meadowlark.

Native sites in our study were sagebrush-steppe, the most prevalent shrubsteppe community remaining in the region (Quigley and Arbelbide 1997). Native grassland communities such as the Palouse Prairie that once covered extensive areas of southeastern Washington have largely been converted to cropland and remain as only a few isolated remnants (Black et al. 1998). Historically, these bunchgrass communities may have supported grassland bird numbers and rates of reproductive success that exceed those presented here for sagebrush-steppe, although historical data for such comparisons are not available. Perennial grass cover on our shrubsteppe sites was high and similar to that in the restored grasslands, a result of the mesic conditions in our study area and a likely explanation for use of these shrubsteppe sites by birds more typical of grassland communities.

Several studies have compared breeding-season use of CRP grasslands planted with native versus exotic grasses by birds in the Midwest (King and Savidge 1995, Delisle and Savidge 1997, McCoy et al. 2001) and Southwest (Thompson et al. 2009), with the general finding that total abundance and species diversity varied little. Some individual bird species were more abundant in 1 type, but the response was often inconsistent and may have been associated with the specific species planted (McCoy et al. 2001, Thompson et al. 2009). Similarly, grassland birds in eastern Washington showed no clear affinity to 1 planting type; the strongest effect was for Savannah sparrow, where abundance estimates were 1.7 times greater in New CRP compared with Old CRP. Most New CRP fields in our study were planted with >1 species of native grass and generally had a more diverse grass component than Old CRP, often including several species of natives and exotics. Monocultures of planted grasses, whether native or exotic, may lack the structure required by some native grassland birds (McCoy et al. 2001, Rodgers and Hoffman 2005) and studies in prairie systems concluded that diverse plantings that include native species likely will enhance restored grasslands for breeding birds (McCoy et al. 2001, Thompson et al. 2009). How breeding birds would respond to restoration efforts using only native grasses and forbs remains to be tested in this region.

Reproductive Success in CRP Grasslands

Ultimately, the value of restored grasslands to avian conservation will be greatest if birds of conservation concern can successfully reproduce and contribute to local populations. In our study, reproductive success of birds in CRP, measured over a suite of parameters, was equal to or greater than that of birds using shrubsteppe. Vander Haegen (2007) modeled population growth of Brewer's sparrows in this region using empirical data for seasonal reproductive success and return rates of banded birds to estimate adult survival. Estimates of seasonal reproductive success for Brewer's sparrows in CRP in the present study were equal to or greater than those from extensive areas of shrubsteppe (Vander Haegen 2007), indicating that CRP grasslands have the potential to contribute to local populations. Landscape factors influence the composition of predator communities, often in complex ways (Tewksbury et al. 1998), and it is likely

that productivity of birds nesting in CRP in landscapes heavily dominated by cropland may be lower than those presented here (Vander Haegen 2007). Seasonal productivity of birds nesting in CRP should be evaluated over a range of landscape contexts to aid in management decisions on where to focus land conservation and restoration efforts.

Several studies have compared nest success of birds in CRP and in other managed grasslands with that of birds nesting in native vegetation communities. Similar to our findings, the general trend in these studies was for equal or greater nest survival in managed grasslands compared with native prairie and shrubsteppe (Clawson and Rotella 1998, McCoy et al. 1999, Howard et al. 2001, Stanley 2009, but see Lloyd and Martin 2005). Management choice between planting exotic versus native grasses also did not influence reproductive parameters on our CRP fields, similar to findings from Oregon, USA, where increasing cover of exotic grasses in pastures of remnant bunchgrass prairie was not associated with nesting success of grassland passerines (Kennedy et al. 2009). Although few vegetation parameters at the nest and site level had strong effects on nest survival rates in our study, those that were strong suggest that increased cover was a benefit.

Vegetation structure rather than the species planted (native vs. exotic) ranked highest in our models of abundance and nest success, suggesting that a focus on planting only native grasses and forbs may not be necessary to benefit some bird populations. This has implications for large-scale restoration where expense and availability of native seeds can be limiting (Knick et al. 2003, Pyke 2011). Wildfire can be devastating in modern shrubsteppe systems, particularly those in low rainfall zones and at low elevation (Knick and Rotenberry 1997, Davies et al. 2012). Rapid establishment of perennial vegetation is a critical step in restoration of these sites to avoid takeover by invasive annuals such as cheatgrass (Bromus *tectorum*), and there may be merit in considering a variety of options, including nonnative grasses, when restoring such areas (Asay et al. 2001, Brown et al. 2008). However, we would argue that the current trend toward planting native grasses and forbs in set-aside programs such as the CRP is a positive step that may provide added benefit to grassland and shrubland birds and is likely of critical importance to some threatened species, such as greater sage-grouse and pygmy rabbit, that consume a diversity of native understory plants (Green and Finders 1980, Connelly et al. 2000, Siegel Thines et al. 2004). Moreover, a focus on planting native species will help shift the ecological trajectory of the landscape away from the current trend toward more exotic plant species and toward increased ecological resiliency (Knick et al. 2003).

MANAGEMENT IMPLICATIONS

Farmland set-aside programs, such as the CRP, establish guidelines for what species will be planted and, hence, what birds are likely to benefit from restoration efforts, and as such can facilitate targeted management to benefit declining species. Establishing sagebrush cover is a critical key to maximizing the benefit of CRP grasslands to shrubland birds in intermountain shrubsteppe ecosystems. Our results suggest that restoring >5% cover of mature sagebrush will be necessary to promote use of CRP by shrubland birds and that use will increase with increasing levels of shrub cover. Sagebrush takes significantly longer than herbaceous plants to achieve a size beneficial to birds; for this reason we suggest that CRP with a well-developed sagebrush component be viewed as a long-term investment. Federal farm programs that emphasize long contracts and that place value in extending contracts where sagebrush cover is adequate will have the greatest opportunity to benefit shrubland birds.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

APPENDIX 1. Model-averaged parameter estimates for variables in models of species abundance in Conservation Reserve Program fields (CRP) planted with exotic bunch-grasses (Old CRP) and with a mix of exotic and native bunchgrasses (New CRP) and in native shrubsteppe habitats in eastern Washington, USA, 2003–2005.

APPENDIX 2. Number of eggs in completed clutches and number of fledglings from successful nests in native shrubsteppe and in Conservation Reserve Program fields (CRP) planted with exotic bunchgrasses (Old CRP) and with a mix of exotic and native bunchgrasses (New CRP) in eastern Washington, USA, 2003–2005.

APPENDIX 3. Odds ratios for parameters from models of daily nest survival for shrubland birds and grassland birds in Conservation Reserve Program fields (CRP) planted with exotic bunchgrasses (Old CRP) and with a mix of exotic and native bunchgrasses (New CRP) and in native shrubsteppe habitats in eastern Washington, USA, 2003–2005.